A NEW FOSSIL HOMOLID CRAB (DECAPODA, BRACHYURA), MIDDLE TERTIARY, SOUTHEASTERN AUSTRALIA

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Summary

JENKINS, R. J. F. (1977).—A new fossil homolid crab (Decapoda, Brachyura), middle Tertinry, southeastern Australia. Trans. R. Soc. S. Aust. 101(1), 1-10, 28 February, 1977.

Two new fossil decapod localities are reported in, respectively, the Oligocene and Miocene of the Mount Gambier area, and a new species of homolid crab, *Paromola pritchardi* sp. nov, is described from fragmentary remains collected at the older of these occurrences. The description of this form provides an opportunity for a review of the genus.

Introduction

In 1953 Professor M. F. Glaessner discovered fossil decapod remains in the Gambier Limestone (Sprigg 1952) near Mount Gambier, South Australia (Fig. 1). A second discovery of fossil decapods in the same formation, and also near Mount Gambier, was made in 1955 by Dr Mary Wade. The Gambier Limestone is of Late Eccene to Miccene age and occurs within the Gambier Embayment, a deep tectonic-sedimentary depression which forms the western part of the Otway Basin in southeastern Australia (Ludbrook 1969). The formation reaches a thickness in excess of 150 m; it consists largely of the fragmented remains of bryozoans and often includes abundant foraminifers (Ludbrook 1961, 1969; Abele 1967),

The discovery made by Glaessner is in the row of building stone quarries on sections 26, 28, 29, 30, 144 and 145, hundred of Blanche, 12 km west of Mount Gambier. Foraminiferal assemblages collected from section 28 and studied by McGowran (1970)¹ and myself suggest a dating within the *Globigerina labiacrassata* zone of Ludbrook & Lindsay (1969) or approximately Zone P. 19/20 of Blow (1970). With reference to Berggren (1972), this is late Early Oligocene. Coccolith studies made on the same samples by Mr S. Shafic were also suggestive of a late Early Oligocene or late Rupelian age (R. J. F. Jenkins 1974). The fossil decapods from this locality are the richest and most diverse assemblage yet known from the Palaeogene of Australia, Either Glaessner or 12 have identified representatives of Pagurus Fabricius Trizopagurus Forest, Munida Leach, Dynomene Latreille, Paromola Wood-Mason & Alcock, Ebalia Leach, Lyreidus de Tutankhamen Leptomithrax Miers, Haan. Rathbun, Ovalipes Rathbun, Nectocarcinus A. Milne-Edwards, Pseudocarcinus H. Milne-Edwards, Carcinoplax H. Milne-Edwards, and Homoioplax Rathbun. Three other unidentified genera are also present.

The decapod remains occur most numerously in the interval of well bedded, coarse grained, pink and yellow, bryozoal limestone which immediately overlies the homogeneous, even grained, white bryozoal limestone cut for building blocks. These limestones are part of the "middle member" of the Gambier Limestone (McGowran 1973).

The occurrence discovered by Dr Wade is in the quarries on sections 601 and 606, hundred of Blanche, 7 km south of Mount Gambier, Foraminiferal studies made by McGowran¹ indicate an age within the later part of the the *Globigerina woodi woodi* zone of Ludbrook & Lindsay (1969) or the *Globigerina woodi* connecta zone of D, G. Jenkins (1967); these

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¹ McGowran, B. (1970).—Age of six samples of Gambier Limestone, Unpublished Geol. Survey Report, Dept Mines, S. Aust. (455), 1-8.

² Jenkins, R. J. F. (1972) —Australian fossil decapod Crustacca: faunal and environmental changes. Ph.D. thesis.



Fig. 1. Southeastern Australia and the Mount Gambier area. The fossil decapod occurrences described are in the quarries on the numbered sections shown on the map of the Mount Gambier area.

datings are in the vicinity of the lower part of Zone N.6 of Blow (1969), or middle Early Miocene. The decapod fauna is less prolific than at the first locality; it includes representatives of Axius Leach, Paguristes Dana, Paromola, Lyreidus, Ovalipes and Nectocarcinus and an unidentified parthenopid.

The crabs mostly occur in the fine grained bryozoal limestone at the bottom of the quarries. Two fragments identified as *Paromola* cf. *pritchardi* are from section 606, one from uncertain level and the other in coarse grained bryozoal limestone from probably high in the exposure. The rocks in the quarries are part of the upper member of the Gambier Limestone.

The repository of the fossil specimens studied is the palaeontological collection of the South Australian Museum (catalogue numbers prefixed "P" in the text). Observations were also made on dried specimens of the extant Paromola petterdi (Grant 1905) in the collection of the South Australian Museum (numbers prefixed "C").

Systematics

Order Decapoda Infraorder Brachyura Section Dromiacea Superfamily Homoloidea Family Homolidae White, 1847

Type-genus: Homola Leach, 1815.

Remarks: Workers such as Ihle (1913), Gordon (1950), and Williamson (1965) have concluded from neontological studies that the division between the Latreilliidae (type-genus *Latreillia* P. Roux, 1830) and the Homolidae is less clear than previously supposed and unite these two families. This unity is rejected by Wright & Collins (1972) on palaeontological grounds; they consider that one of the most important diagnostic features of the Homolidae

Footnote added in proof: The following publication was not seen.

Serene, R. & Lohavanijaya, P. (1973).—The Brachyura (Crustacea: Decapoda) collected by the Naga Expedition, including a review of the Homolidae. Naga Rep. 4(4), 1-187.

is the presence of dorsal *lineae homolicae*, and indicate that these structures are absent in *Latreillia* and not present in other Cretaceous forms which they refer to the Latreilliidae. They conclude that the Homolidae and Latreilliidae "have probably been independent stocks since Upper Jurassic times, albeit developing to some extent in parallel". This viewpoint is accepted herein.

Wright & Collins (1972, p. 31) consider that Latreillapsir Henderson, 1888, which does have lineae, is probably not allied to Larreillia, but is a homolid.

Genus Paromola Wood-Mason & Alcock, 1891

Type species: Dorippe cuvieri Risso, 1816, by munotypy.

- Paromola Wood-Mason & Alcock, 1891: 267: Rathbun, 1937: 68; Bouvier, 1940: 190; Gordon, 1950: 222; Griffin, 1965: 86 (but not the new species thereunder described); Alvarez, 1968: 301.
- Homola (Paromola) Alcock, 1899: 156; 1901: 64; Ihle, 1913: 69 (in key); Sakai, 1936: 47.
- Thelxiope (Moloha) Barnard, 1946: 371: 1950: 341.

Diagnosis: Carapace urn-shaped or subrectangular, longer than broad, widest across branchial regions; rostrum a simple spine flanked on either side by a single supraorbital spine (occasionally with small side branches) of equal or greater size; *lineae homolicae* conspicuous, well inside lateral margins; surface usually granulate with scattered spinules, spines and tubercles, smooth in one extant species. Merus of third maxilliped elongate with a dentate prominence or a spine near middle of length of outer margin; inner margin of joint usually denticulate. Meri of pereiopods usually spinose along their length. Palms of chelae of 1st pair of pereiopods smooth or granulate. Extant species with 13-14 gills plus 5-6 epipods.

Remarks: In the literature *Paromola* has often been confused with two other genera of homolids, *Homola* Leach, 1815 (= *Thelxiope* Rafinesque, 1814) and *Latreillopsis* Henderson, 1888. These genera all have an urn-shaped or sub-rectangular carapace and slender, elongate perelopods.

In *Paromola* and *Homola* the meri of the pereiopods are spinose. The branchial formula of extant species of *Homola* is 13-14 gills + 6 epipods, similar to or little different from that in *Paromola* (see Bouvier 1940, p. 191-193; and Gordon 1950, p. 220-221). Differences between the two are indicated in Table 1.

The extant, New Zealand Paromola spinimana Griffin, 1965, which has two prominent spines above each orbit, a conspicuous spine on each epigastric region, and the palms of the chelipeds spinose, is referable to Homola.

The genus Larreillopsis has as its typespecies the extant, Indo-West-Pacific Latreillopsis bispinosa Henderson, 1888. This, and a second living species, the Japanese Latreillopsis laciniata Sakai, 1936, are distinguished from Paromola by their branchial formula of 10 gills plus four epipods (Gordon 1950, p. 220). However the gill structure is not preserved in fossils. External morphological differences between these two species and members of Paromola are given in Table 2.

The following previously described extant species have been included in *Paromola* or appear referable to this genus;

Paromola cuvieri (Risso 1816)

Mediterranean (excluding the Adriatic) and eastern Atlantic, from Angola, Cape Bojador and the Azores north to Cork, the Shetland Is.

TABLE I

Summary of differences distinguishing Paromola Wood-Mason & Alcock, 1891, from Homola Leach, 1865.

Character	Homola	Paromola A single spine projects above each orbit	
Supraorbital spines	Two spines project above each orbit, a lateral rostral spine near base of rostrum, and a second spine more lateral		
Rostrum	Usually bidentate, less commonly single	Invariably single	
Epigastric tubercles or spines	A prominent lubercle or spine is situated on each epigastric region behind lateral rostral spine	Epigastric regions usually without conspicuous tubercles or spines	
Chelac of 1st pair of perclopods	Palms usually spinose	Palms either smooth or bearing pointed granules	

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Summary of external skeletal differences distinguishing Paromola from Latreillopsis

Character	Latreillopsis	Paromola	
Surface of carapace	Upper surface wrinkled with few distinct tubercles	Usually spinose with granules and pointed tubercles between	
Width of carapace	Apparently mature individuals widest across hepatic regions, which are very swollen	Except in juveniles, carapace widest across branchial regions	
Third maxilliped	Merus quadrate in shape; both merus and ischium without spines	Merus elongate, with dentate pro- minence or spine about midway along its outer margin; external distal angle of ischium sometimes produced to a spine; inner margin of both joints usually denticulate	
1st pair of perelopods (cheli- peds)	Merus bearing only a terminal spine	Merus spinose along length in most species	

and west coast of Norway; 150-1320 m, rarely in shallower waters.

Paromola projundorum (Alcock & Anderson 1899)

Travancore coast of India; 786 m. Maldive area; 256 m Eastern coast of Africa; 1362 m.

Paromola petterdi (Grant 1905)

Figs 31 & 4G-H.

Paromola petterdi-Gordon, 1950: 220.

Southern and southeastern Australia, from near Grafton south to Bruny I., Tasmania, and west to Eucla; 91–1460 m. North Island of New Zealand from the Cavalli Is. to Banks Peninsula; 183-541 m. The specimen photographed, d, C 83, is from 32 km S.W. of Cape Everard, Victoria, at a depth of 164 m.

Paromola rathbuni Porter, 1908

Isla de Mas-Afuera, Juan Fernández, Chile.

Latreillopsis multispinosa Ihle, 1912.

Latreillopsis multispinosa Thle, 1912; 78, pl. 4, figs 19-21. Kei Is.; 204 m

This species is referable to *Paromola* because of the numerous long spines on its carapace and the form of the third maxillipeds, which have an elongate merus with a lateral spine and a terminal spine on the ischium. It markedly resembles and is evidently a near relative of *Paromola acutispina* (Sakai 1962) from Japan.

Paromola japonica Parisi, 1915

[= Latreillopsis hawaiiensis Edmondson, 1932] Japan: Tanega Shima I., Izu Peninsula, Sagami Bay: 183-392 m. Hawaii; 55 m. According to Sakai (1936) the species inhabits a rocky bottom. Paromola alcocki (Stebbing 1920)

[Apparently = Latreillopsis major Kubo, 1936; ? = Homola (Parhomola) majora Edmondson, 1951.]

Southern Africa: Algoa Bay, South Africa; Mozambique; 73–312 m. Maldive area: 229 m. Japan [*Paromola major* (Kubo)]: Izu Peninsula, Sagami Bay, Tokyo Bay; 100–200 m. ?Hawaii [*Homola (Parhamola) majora* Edmondson]; 12-107 m. The Japanese form inhabits a muddy bottom (Sakai 1936).

Paromola faxoni (Schmitt 1921)

Off San Diego, California: 122-370 m. A remarkable photograph of this species in its natural environment at a depth of 370 m (Church 1971, p. 113) shows the subchelate hind limbs holding a piece of sponge above the back of the animal.

Paromola macrochira Sakai, 1962

Japan: Tosa Bay and Kii Peninsula.

Homola (Moloha) acutispinosa Sakai, 1962

Homola (Moloha) acutispinosa Sakai, 1962; 147, pl. 4 fig. 4.

Japan: Tosa Bay.

Characters of this species which indicate that it is referable to *Paromola* are the single large spine above each orbit, single rostrum, absence of epigastric spines and the smooth palms of the chelipeds.

One previously described fossil species can probable be referred to *Paromola*;

Homolopsis japonicus Yokoyama, 1911

Homolopsis japonicus Yokoyama, 1911: 12, pl. 3, fig. 4.

Paleocene or Eocene: Milke Coalfield, Japan.

The single median portion of a carapace from which this species was described unfortunately has the frontoorbital region damaged, but closely resembles *P. pritchardi* and *P. petterdi* in the shape of the other regions and in the positioning of the major tubercles.

The modern species belonging to Paromola can be divided into three informal speciesgroups which may be characterized as follows:

- P. cuvieri group. Carapace more or less covered by granules and spinules and bearing short to moderately long spines on lateral and anterior-dorsal aspects. Palms of chelipeds smooth or bearing pointed granules, particularly in mature individuals. P. cuvieri, P. petterdi, P. rathbuai, P. japonica, P. alcocki, P. faxoni, P. macrochira.
- P. profundorum group. Catapace mainly smooth, with one hepatic spine and one denticle on branchial margin. Palms of chelipeds smooth P. profundorum.
- P. muhispinosa group. Carapace bearing clongate spines, between which it is mainly smooth. Palms of chelipeds smooth. P. multispinosa, P. acutispinosa.

The early Tertiary *Paromola japonicus* (Yokoyama) is a fossil member of the *P*. *cuvieri* group.

> Paromola pritchardi sp. nov. Figs 2, 3A-O, & 4A-E

Nume: Named after Pritchards Quarry, on section 28, hundred of Blanche, South Australia.

Material: Seventeen incomplete specimens of various parts of the carapace and four specimens of isolated abdominal tergites. Holotype, P15631. Median part of carapace with rostrum and supraorbital spines lacking.

Occurrence: Gambier Limestone in quarries on sections 26, 28 and 30, hundred of Blanche.

Age: Late Early Oligocene.

Description: Carapace subrectangular, gently convex above, extremely deep in lateral aspect; regions well marked, delimited and subdivided by moderately deep grooves; greater part of surface covered by variably sized granules and spinules, nine short spines on dorsum in advance of cervical groove, lateral aspects of carapace ornamented by short spines and blunt spinules. Portion of carapace between *lineae* homolicae 1.5 times as long as wide, broadest across mesobranchial regions.

Rostrum a single, forwardly directed, slender spine about a sixth length of carapace, slightly deflexed basally, smoothly upcurved distally,



Fig. 2. Paromola pritchardi sp. nov., reconstruction of carapace; lettering indicates regions: O, supraorbital; Eg, epigastric; Pg, protogastric, 1, anteromedial lobe, 2, anterolateral lobe, 3, posterolateral lobe; H, hepatic; Mg, mesogastric; M, metagastric; Eb, epibranchial; Ib, inner-branchial lobe; U, urogastric; C, cardiac; Mb, mesobranchial; Mt, metabranchial; I, intestinal. Approximately x3.

Orbits forwardly directed and with a large supraorbital spine above; inner part of supraorbital margin smoothly concave and with a narrow border; supraorbital spine directed obliquely upwards, forwards and slightly outwards, about twice length of rostrum, with a lateral spinule at about half length; a short spine on lower corner of lateral margin of orbit.

Epigastric regions relatively small, slightly raised, with only a few granules. Protogastric regions each subdivided into three lobes by an oblique Y-shaped groove; anteromedial lobe with a central spine and two spinules on posterior part, anterolateral lobe with a single prominent spine; posterolateral lobe with a prominent spine on lateral aspect, a lesser spine on inner portion, and several small spinules between. Hepatic regions strongly inflated, bearing a crescentic row of four acute spines on anterolateral aspect and a group of spinules behind. Mesogastric region with a median spine set at centre of a circlet of five, or a triangular arrangement of three small spinules; a pair of granulate ridges adjacent to posterior margin of region. Cervical groove strongly impressed. containing slit-like posterior gastric pits at .50-.52 length of carapace. Metagastric region in form of two oblique, elongated, granulate lobes and with a pair of more prominent granules positioned submedially. Urogastric region saddle-shaped, its lateral margins marked by two incised, crescentic grooves. Cardiac region moderately inflated, subtriangular, with three prominences, two side by side before and one behind. Intestinal region depressed, progresbroadened reatwards. Epibranchial sively regions obliquely elongated, with a spine just outside lineae homolicae and an irregular line of spinules on lateral aspect. Inner-branchial lobes on either side of urogastric region obliquely elongated and with one more prominent granule. Branchiocardiac groove well marked. Mesobranchial regions gently inflated, each with a line of at least three short spines just outside lineae homolicae, most anterior of these spines the largest and situated on a slight ridge behind lateral portion of branchiocardiac groove. Metabranchial regions relatively small, two-lobed, with a spinule on posterolateral portion of Inner lobe. Subbranchial margin with a narrow border. Posterior margin fairly wide, raised, with median third indented.

A spinule at anterolateral corner of buccal frame.

Muscle attachment scars only faintly marked on interior surface of carapace except for the two small depressions forming the gastric apodemes.

Third and fifth segments of male abdomen each with a prominent median lobe and a spinule at centre of each of the lateral lobes. Fifth segment subrectangular, with posterior angles slightly produced; median lobe apparently bearing a few scattered granules and with a spinule on anterior portion; lateral lobes obliquely sulcate and apparently ornamented by coarse granules. Fourth segment of female abdomen with the lateral lobes slightly inflated and curved downwards (if abdomen was straightened behind crab) and the surface nearly smooth except for a few, scattered weak granules; an obscure tubercle on anterior portion of median lobe,

Measurements: Holotype (P15631), length of carapace excluding rostrum, 18 mm; width of median part of carapace between lineae homolicae at level of mesobranchial regions, 12 mm. Paratype (P15632), length of carapace excluding rostrum, 23 mm; length of rostrum (incomplete), 3.6 mm; width of median part of carapace between lineae homolicae at level of mesobranchial regions, 16 mm. The largest individual known is represented by an incomplete carapace (paratype P15638) approximately 1.3 times the size of that of P15632.

Remarks: The precise arrangement of the minor spinules on the carapace of *P. pritchardl* is very variable and the relief of the regions also varies slightly in different specimens.

F. pritchardi belongs to the P. cuvieri species-group and closely resembles P. petterdi and P. alcocki. It seems slightly more similar to P. petterdi than to P. alcocki, but is possibly ancestral to both. It differs from P. petterdi in the more rectangular shape of its carapace, its more uplurned rostrum, and in the less prosculpture of the mesobranchial nounced regions. The posterior gastric pits are situated at about .50-.52 the length of the carapace in P. pritchardi, but at about .41-.43 the length in P. petterdi. As well, the fossil species has a prominent spine on the anterolateral lobe of the protogastric regions, while only a small lubercle is situated in this position in P. petterdi.

The fossil species differs from *P. alcocki* again in its more rectangular carapace, and in having longer supraorbital spines and many fewer spinules present on the branchial regions. *P. alcocki* has the posterior gastric pits situated at about .43 the length of the carapace.

P. pritchardi apparently differs from the Eocene or Paleocene Paromolu japonicus

Fig. 3. A-G—Paromola pritchardi sp. nov. A, holotype, P15631, median part of carapace, dorsal view, x3; B, paratype, P15632, median part of carapace, dorsal view, x2,5; C-D, paratype, P15637, latersl part of carapace, with spinule(s) on lower corner of latersl margin of orbit, left side, C, dorsal view, x3, D, latersl view, x3; E-F, paratype, P15636, fragment broken from latersl part of carapace, left side, E, dorsal view, x3, F, latersl view, x3; G, paratype, P15639, fragmentary remains of median part of carapace with rostrum and one supraorbital spine present, view of interior surface, x2.

H—Paramala cl. pritchardi P15806, fragment of median part of carapace, view of interior surface, x24.

1-Paromola petterdi (Grant 1905), Specimen C83, & dorsal view, x1.4.

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(Yokoyama) in lacking a distinct transverse ridge over the anterior part of each mesobranchial region and in bearing several additional spines. The differences which occur between P. japonicus and P. pritchardi, and between these fossils and the modern species, P. petterdi and P. alcocki, seem relatively minor and are indicative of an extremely slow rate of evolutionary change. If this rate of change is at all comparable to rates of evolutionary change experienced by Paromola prior to the Eocene or Paleocene, then the genus may date from a much earlier time, probably from within the Mesozoic. The fossil record of the Homolidae extends back to the Late Jurassic (Glaessner 1969). None of the other fossil genera of homolids yet described appears likely to be the direct ancestor of Paromola.

Paromola cf. pritchardi Figs 3H & 4F

Material: A fragment of the median part of a carapace, P15806, and a fragment of the lateral part of a carapace, P15805.

Occurrence: Both specimens from Gambier Limestone in quarry on section 606, hundred of Blanche; P15806 from a loose piece of rock 3.5 m below the ground surface.

Age: Middle Early Miocene.

Measurements: P15806, width of median part of carapace between lineae homolicae, approximately 13 mm. P15805, height of lateral part of carapace approximately 8 mm.

Remarks: These remains are too fragmentary to be positively identified to the level of species, but in all features closely resemble the corresponding parts of P. pritchardi.

Palaeoecology

The abundance of planktonic foraminifers in the Gambier Limestone (though not at the fossil decapod locality 12 km west of Mount Gambier) is indicative of an open marine environment of deposition (Ludbrook 1961). The scarcity of terrigenous detritus in the formation, particularly the middle member,

shows that it accumulated in very clear waters. Slender branching forms of bryozoans comprise the major component of the limestone (Abele 1967). In the present day seas of southern Australia, living bryozoans abound at depths of 90-220 m, and their remains are accumulating as sediments over wide areas of the continental shelf and the upper part of the continental slope (Conolly & von der Borch 1967: Wass, Conolly & MacIntyre 1970). Many of these sediments strikingly resemble those composing the Gambier Limestone in the kinds of bryozoans present, the proportions of foraminifers and other skeletal remains (such as molluses, echinoids, and serpulid worms), their degree of sorting, and in the associated sedimentary structures (current ripples and mounds). It seems reasonable to suppose that the Gambier Limestone is a fossil equivalent of these deposits and that it formed in waters of comparable depth (approximately 90 to 220 m). This view contrasts to some degree with that of Abele (1967) who noted that the shape of certain foraminifers present in the formation is characteristic of forms which live attached to seaweed. He inferred that deposition occurred between approximately 40 and 100 m depth.

The range of depth of deposition suggested above overlaps the depth range in which the extant species of Paromola are most frequently recorded, between approximately 100 and 500 m. Thus P. pritchardi probably lived at similar depths as modern members of the genus. The living species to which the other fossil decapods known from the Gammer Limestone are most closely allied, also occur typically on the outer part of the continental shelf or on the upper part of the continental slope. Photographs of the sea bottom in the areas just mentioned (Conolly & von der Borch 1967; Wass, Conolly & MacIntyre, 1970) show living bryozoans occurring in forests and associated with spouges, or more sparsely distributed on open areas of sediment, Paromola seems well adapted to live in bryozoan forests, its long

Fig. 4. A-E—Paromola pritchardi sp. nov. A, paratype, P15643, hepatic region of carapace, right side, with a spinule(s) on the part of the margin corresponding to the anterolateral corner of the buccal frame, lateral view, x2.5; B, paratype, P15635, incomplete lateral part of carapace, right side, lateral view, x3; C, paratype d, P15640, tergite of third segment of abdomen, view of interior surface (top anterior), x6; D, paratype d, P15641, tergite of fifth segment of abdomen, view of interior surface (top anterior), x3; E, paratype 9, P15634, tergite of fourth segment of abdomen, external surface (top anterior), x2.5.

F-Paramola cf. pritchardi P15805, fragment of lateral part of carapace, left side, lateral view, x3.5.

G-H-Paromolo petterdl (Grant, 1905). Specimen C83, 2, G. anterior-ventral aspect, x6, H. dorsal view, x2.5.

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legs and high stance (Church 1971: fig. on p. 113) probably enabling it to step over the bryozoans.

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pod occurrences which they discovered; Professor Glaessner is also thanked for his constructive criticism of the manuscript. Dr B. McGowran, University of Adelaide, kindly examined and provided age data on various foraminiferal samples.

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